Bird Communities and Vegetation on Swedish Wet Meadows

Importance of Management Regimes and Landscape Composition

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Abstract

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Wet meadows in Sweden currently depend on management by grazing to maintain habitats for various breeding and migrating birds. However, due to ceased cattle farming management by mowing could be an option for restoration and conservation of wet meadows. The general aim of this thesis is to analyse effects of different management regimes (mowing and grazing), landscape composition and flooding on inland wet meadow bird fauna and flora. Five wet meadow areas in southern Sweden were used for a four-year survey of breeding birds and environmental variables. Habitat openness was the most important factor for bird community composition. Species preferring open meadows decreased strongly in abundance at small amounts of forest, suggesting that clearing of woodlands could be important. The bird community was also strongly related to the amount of flooding. Effects of management were weaker, but several species showed positive associations with swards of intermediate height (5-30 cm), which are correlated to mowing with late season grazing. In addition, measures for restoring water table variation also need to be considered. Conservation of species dependent on continuous management (yearly grazing, mowing and late season grazing) and short swards should be targeted to large open meadows. Corncrakes preferred unmanaged meadows with tall vegetation, suggesting that mowing at intervals of a few years could be appropriate. Yellow Wagtails are likely to have higher breeding success in mowed than in grazed sites due to lack of nest destruction by livestock. The main gradients affecting distribution of vascular plants correlated to soil fertility and moist. Bird species associated with weak or no management correlated positively to nutrient levels, soil reaction, sward height and litter depth. In contrast, the assembly of bird species associated with continuous management, showed fewer associations to the sward variables, although their abundance was positively associated with abundance of forbs. Different mowing regimes may be a useful tool for management of meadow sward heterogeneity.

Keywords: Wet meadow, mowing, grazing, bird censuses, Corncrake, Yellow Wagtail, vascular plants, soil nutrients, humidity, management history, edge effects, nest predation, trampling, artificial nests.

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Appendix

Papers I-IV

The thesis is based on the following papers, which will be referred to by their Roman numerals:

I. Gustafson, T. and Berg, Å. Meadow birds on Swedish inland wet meadows - effects of landscape structure, flooding and management. *Manuscript*

II. Berg, Å. and Gustafson, T. Meadow management and occurrence of corncrake *Crex crex.* Agriculture, Environment & Ecosystems. *In press.*

III. Gustafson, T. and Berg, Å. Breeding success and abundance of Yellow Wagtail on wet meadows managed by grazing or mowing. *Manuscript*.

IV. Gustafson, T. and Berg, Å. Sward composition and bird fauna on an inland wet meadow - effects of moisture, nutrient levels and management history. *Manuscript.*

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As first author of Paper I, Paper III and Paper IV, I contributed with major parts of study set up, field work, data analysis and preparing of papers. As second author of Paper II, I contributed to study set up and field work, was responsible for the data analyses and contributed to the preparing of the paper.

Introduction

Management of wet seminatural grasslands (i.e. wet meadows) by grazing or mowing maintains this habitat suitable to a large range of different organisms (Joyce and Wade, 1998) although focus has mainly been on the conservation of bird diversity (e.g. Tucker and Heath, 1994). However, the area of wet meadow habitats has been reduced strongly because of drainage of wetlands and cultivation (i.e. conversion of meadows to arable fields). Furthermore, habitat quality for breeding birds has declined due to earlier hay cutting and higher stocking of cattle (e.g. Beintema and Müskens, 1987; Hötker, 1991; Chamberlain and Fuller, 2000). During the period 1990-2000, 39% of European bird species of inland wetlands declined in numbers (BirdLife International, 2004). Many Swedish wet meadow birds have declined in numbers during recent decades (Lindström and Svensson, 2006). Today, at least 15% of all red-listed Swedish bird species depend on combinations of farmland and regularly managed wetland-grassland habitats, such as the Curlew *Numenius arquata* and the Corncrake *Crex crex* (Gärdenfors, 2005).

In farmland plains of southern Sweden the area of wetlands were considerably reduced during the late 19th – early 20th centuries; because of intense drainage for cultivation 90% of the wetlands disappeared (Bernes, 1993). The open wet meadow was reduced further by ceased livestock farming and by the use of arable fields for grazing and fodder production (Emanuelsson and Johansson, 1987; SJV, 1999). Ceased management has been suggested to be the main cause of declining meadow bird populations in Sweden (Andersson, 1988). Additionally, lack of water level fluctuations due to drainage systems has resulted in spread of reeds on former open wetlands and shallow waters (Bernes, 1993).

During the 1990s, the number of restoration projects on semi-natural grasslands increased, especially on wet meadows. In 1999 the Swedish Parliament decided to: a) conserve and maintain all seminatural pastures and mown meadows in Sweden (450 000 hectares) and b) construct or to restore 12 000 hectares of wetlands and ponds in farmland to increase farmland biodiversity (SEPA, 2005). Subsidies have financed many restoration projects, and subsidies are also important for the maintenance of the management on remaining wet meadows (SJV, 1999; Stenseke, 2004). However, the general effects on biodiversity of agro-environmental schemes have been debated (Kleijn et al., 2004). A Dutch study of the effects of "meadow bird agreements" between farmers and authorities (i.e. postponed first date for agricultural activities on meadows) found that population trends for selected meadow birds between sites with and without agreements did not differ, probably because the schemes not were targeted at areas with the most appropriate soil moisture conditions (Kleijn and Zuijlen, 2004). The Swedish allowance guidelines have required intensive yearly management, although the effects of different management regimes on the occurrence and abundance of breeding meadow birds are poorly known (Chamberlain and Fuller, 2000; Hellström and Berg, 2001; Vickery et al., 2001; Evans, 2004; McCracken and Tallowin, 2004).

Wet meadow management currently depends on grazing animals, whereas mowing is confined to large and regionally scattered sites covering less than 15% of the total wet meadow area (SJV, 2005). However, mowing may be an important alternative management strategy in the future. In central Sweden management-dependent species (e.g. waders) and the Corncrake (a species preferring tall swards) occur in the same meadow sites. Thus, management of wet meadows supported by subsidies should benefit both species preferring short vegetation, such as the Lapwing *Vanellus vanellus* (Klomp, 1954) and other waders, and species preferring tall vegetation such as the corncrake. In Swedish mosaic landscapes with woodlands the amount of forest have been shown to have a large influence on the bird community composition (Pärt and Söderström, 1999; Berg 2002). However, the relative importance of management, landscape structure, amount of flooding and other habitat characteristics for the meadow bird fauna is poorly known. In large meadow areas, it should be possible to combine management strategies that are beneficial for species preferring different management regimes. However, more detailed knowledge about different species preferences for different management regimes, other habitat factors and flooding are needed.

The general aim of this thesis is to contribute to increased knowledge about effects of management regimes, flooding and landscape structure on the meadow bird fauna and flora.

More specifically the aims are:

i) to quantify effects of grazing, mowing, and mowing with late season grazing on the wet meadow bird fauna and flora.

ii) to quantify effects of the surrounding landscape composition and relative importance of spring flooding levels.

iii) to quantify effects of management history (e.g. number of years managed after restoration) on the meadow fauna and flora.

iv) to identify potential mechanisms behind changes in abundance by detailed studies of habitat selection and reproduction of selected "model bird" species (Corncrake *Crex crex* and Yellow Wagtail *Motacilla flava flava*).

Study areas and methods

Study areas

Five meadow areas (Vattenriket, Roxen, Hjästaviken, Fyrisån and Svartån) were selected as study sites. The meadow bird censuses (Paper I) were performed in all five areas, the corncrake study (Paper II) was performed in the Svartå and Fyriså areas, while the Yellow Wagtail (Paper III) and vegetation studies (Paper IV) were restricted to parts of the Svartå site. The meadows areas are distributed from south Sweden (county of Skåne) to south central Sweden (county of Västmanland). The arable fields were flooded during spring and were used either for grazing (i.e. cultivated pasture) or crop cultivation. Grazing was the dominant management regime in most meadows areas, but at the Svartån area mowing was the dominant management regime. Mowing was also used at Vattenriket and Fyrisån, while grazing was the only management regime at Roxen and Hjälstaviken. Water level variation was larger, and length of the growing season longer in the two southern wetland areas (Vattenriket and Roxen), see Table 1. However, Hjälstaviken and Roxen had the wettest sites. The sites at the five areas differed significantly also in habitat composition, such as sward height, soil types and landscape composition (see Appendix 1 in Paper I).

Table 1. Description of the five meadow areas: coordinates, area of wet meadow habitat (ha), number of censused sites, water level variation (var., amplitude in m; * denotes dam regulation), yearly precipitation (in mm x 100) and length of vegetation period per year (days, 7-day-mean >3-5°C).

	Wetland area				
	Vattenriket	Roxen	Hjälstaviken	Fyrisån	Svartån
Coordinates	55°59′/ 14°12′	58°29′/ 15°33′	59°40′/ 17°23′	59°50′/ 17°39′	59°56′/ 16°17′
Meadow (ha)	1400	200	210	50	670
No. of sites	38	20	17	13	49
Water level var.	1.4	1	1*	0.5	0.7
Precipitation	6-7	6-7	5-6	5-6	7-8
Vegetation days	200	190	180	180	170

The meadow sites consisted of seminatural vegetation (e.g. dominance of Sedge species *Carex spp*. and Grass species *Poaceae spp*., see description below). Meadows were managed according to criteria of conservation programmes, i.e. mowing was usually done in the second half of July. The grazing season started between May 1 and June 5, with large variation between years and farmers. Three main components of the wet meadow vegetation were distinguished in the study areas, according to Pehrsson (1992) and Påhlsson (1998): a) Tall Sedge meadow type: Frequent species were *Carex acuta*, *Agrostis canina* and *Galium palustre*. The vegetation type was abundant in the wettest sites with high groundwater tables close to open water. Intense grazing gradually increases the abundance of lower plants such as *Agrostis stolonifera*. b) Grass-Short Sedge meadow type: Frequent species were *Carex nigra*, *Carex panicea* and *Molinia caerulea*. This low vegetation type depend on continuous management and was often restricted to narrow zones between the Tall Sedge and Tufted hair-grass vegetation zones. c) Tufted Hair-grass meadow type: Frequent species were *Deschampsia cespitosa*, *Poa pratensis*, *Ranunculus acris* and *Rumex acetosa*. This vegetation type was abundant on moist, unsorted soils.

Methods

Meadow bird censuses (Paper I)

During 2001-2004 investigations of breeding wet meadow birds and habitat composition were performed at the five selected wetland areas. Within these areas a total of 137 wet meadow sites were censused. Management by grazing occurred in101 sites, by mowing in 43 sites, by mowing with late season grazing in 29 sites, while 18 sites were unmanaged. Breeding meadow birds and habitat variables were surveyed each year according to a point census method (Hellström and Berg, 2001), at one visit in each of the periods May 5-20, May 21-June 5 and June 6-20. Censuses were performed during early mornings, from sunrise to 10 AM, from the centre of circle-shaped areas (radius=100 m, i.e. 3.1 hectares). A minimum distance of 400 m between census points was kept to reduce the risk of double counting. At each visit observations were made on the number of breeding pairs of different species during five minutes. Territories were indicated by warning behaviours, song of males and observations of pairs. Because of few visits, local density was estimated as the maximum number of observed breeding pairs every year. In each census point, management, habitat (e.g. flooding, sward height) and landscape characteristics (e.g. distance to different habitats) were mapped during bird censuses (see Appendix 1 in Paper I). Cover of different soil types (SGU, 1975-1998), land use and main habitat composition, e.g. arable land, permanent grassland, forest (Lantmäteriet, 2004; SJV, 2002-2003) within 250 m radius of each census point (19.6 ha) were quantified by use of GIS tools (ArcView GIS 8.0).

Corncrake censuses (Paper II)

All arable fields and meadows at the Svartån and Fyrisån study sites were censused for calling Corncrake males with territory mapping (Bibby et al., 1992). Censuses were performed during four nights (22.00-05.00) in spring (15 May-25 June) each year during 1999-2002. The position of all calling males was recorded on maps. All sites with at least two observations within 100 m were classified as territories. The habitat was classified as cereal crop, set-aside (both rotational and permanent fallows), ley (sown, cultivated grassland with grass or clover), abandoned wet meadow (usually unmanaged for more than ten years), wet meadow used for mowing or meadow used for grazing. Habitat selection of Corncrakes on meadows was analysed by comparing habitat composition within territories and random meadow sites (radius of 200 m). These sites were randomly selected from a 100x100-m grid system covering the two meadow areas. Fifty-two random sites (13 new sites each year) were situated in the Svartån site and 32 (eight new sites every year) in the Fyrisån site. The proportion of arable land, wetland and the proportion of meadows with different management regimes (grazing, mowing or unmanaged meadow) were estimated within territories and random sites. Distance to nearest forest edge and nearest wetland (river or lake) was also measured. The vegetation height was measured with a measurement stick (Stewart et al., 2001) at sites with calling corncrakes and in the centre of all random sites. A single vegetation height measurement was made at each site in order to reflect major differences in vegetation height between habitats. The measurement was made within five days of the first observation in each territory (20 May-5 June) at the location (<10 m) of the calling corncrake (by use of distance to landmarks and field edges).

Yellow wagtail study (Paper III)

Investigation of breeding density of Yellow Wagtails was performed during 2001-2004, according to a point-census method (see methods Paper I above). Yellow Wagtail territories were indicated by warning behaviours of pairs (i.e. intense calling and fluttering above) and song of males. Since breeding Yellow Wagtails frequently moved out of census points to forage and because of few visits, density was estimated as the maximum number of observed breeding pairs every year.

Detailed observations of Yellow Wagtail breeding performance were made during 2002-2003 in nine grazed meadows and 16 mowed meadows, with previous records of breeding Yellow Wagtails (Berg and Ström, 1998). The minimum distance between census site borders was 200 m to reduce the risk of exchange of individuals between sites. At each site 7-14 visits were made (mornings and evenings) from the beginning of May to the end of June, during which the number of breeding pairs was recorded. Because surveys of Yellow Wagtail nests on meadows are difficult and time consuming, indirect evidence for breeding attempts was used. The criterion used for successful breeding attempt was repeated observations (minimum of five observations) of breeding behaviour (Smith, 1950; Dittberner and Dittberner, 1984). From mid May to end of May, a breeding attempt was indicated by male-female interactions (e.g. courtship), territory defence, nest building, and anti-predator behaviour (at least two of these criteria were fulfilled in all territories). In end of May to early June, indications of breeding attempt also included observations of transports of food items to assumed nest sites (in a majority of the territories). A few territories (n=5) were excluded due lack of indications of breeding, and most of these were probably single males without females. Observations of feeding of young or fledged juveniles in June were used as criteria for successful nesting attempt. Yellow Wagtail breeding success was calculated as the proportion of successful nesting attempts.

Environmental variables included management type (grazing or mowing), vegetation structure and distance to nearest permanent water, settlement, forest and arable land. To be able to analyse effects of management intensity on Yellow Wagtail breeding performance and artificial nests (see below), vegetation was classified in five vegetation structure categories within a radius of 15 m of experimental nest sites (see Paper III).

The meadows used for observations of Yellow Wagtail nesting performance were also used for an experiment with artificial nests during 2002-2003. To reduce the risk of interactions and exchange of nest predators, the distance between experimental sites was on average 710 m (SD=$\pm$318 m). To account for possible differences in nest predation rates early and late in the breeding season, the experiment was performed during two periods each year, May 30-June 12 and June 18-July 10. The duration (13 days) and timing of the early period was adjusted to average incubation time of Yellow Wagtails (Cramp, 1988) and regional spring arrival date (Fredriksson and Tjernberg, 1996). Six days were included between the two periods to reduce the risk of learning by predators since e.g. corvids may adjust foraging efforts to human activities (Götmark and Åhlund, 1984). The duration of the late period (22 days) was prolonged compared to the early period due to the low predation rate in the early period during the first year. Thus, the late period corresponded to the estimated time for making of a replacement clutch after predation, the incubation period and parts of the nestling phase in total ca. 29 days (Mason and Lyczynski, 1980; Cramp, 1988).

The artificial nests were constructed by using chicken-wire formed into a shallow basket to closely mimic real nest cups. Two small eggs of Japanese Quail *Coturnix japonica* were placed in each nest together with a plasticine egg of natural egg size. The plasticine egg was anchored in the nest with a short thin wire in order to allow identification of nest predators (from imprints of teeth or bills). In order to prevent predators from removing nests, each nest was attached to the ground by a large nail connected to the nest cup by a metal wire, covered by litter and plants. Three artificial nests were placed in each of the 25 meadows each year, which made a total of 27 nests per period in grazed meadows and 48 nests per period in mowed meadows. Distance between the artificial nests was about 15 m (mean +SD=14.9 +3.8 m), which is close to minimum nest distances of Yellow Wagtails (Dittberner and Dittberner, 1984; Flyckt, 1999), for details see Paper III.

Vegetation study (Paper IV)

The study area Nötmyran is situated in Svartådalen (N59°56′ E16°17′) in the northwest of the county of Västmanland (see also Paper I-III). Nötmyran is located along 4 km of the river Svartån between 58 -59 m.a.s.l., and consists of 340 ha wetland out of which 260 hectares are managed wet meadow (Eriksson, 1978; Berg and Ström, 1998). The management regimes are mowing (150 ha), grazing (50 ha) and mowing in combination with late season grazing (60 ha). All meadow sites are usually flooded during the period April 10th-May 10th and the water level amplitude is about 0.7 m (Berg and Ström, 1998). The soil consists of fen peat, commonly down to at least 90 cm depth where thin gyttja on clay is found (Eriksson, 1978), for details see Paper IV.

Twenty-one meadow sites were selected to get a representative sample of wet meadow swards on Nötmyran. Sixteen sites managed by mowing, three sites with grazing and two sites with no management were investigated. Censuses of vascular plants were performed within circles with 100 m radius (3.1 hectares) at least 300 m apart from each other. In each census site 21 plots defined by a quadratic wood frame (0.5 m^2, with four 0.125 m^2 subplots) were evenly distributed with aid of four crossed transects. Abundances of all vascular plants in plots were estimated by presence-absence in the four subplots. In each subplot assessments were also made of sward height, depth of litter and cover of mosses, bare ground and presence/absence of tree or shrub canopy. Records on management of meadow sites (Eriksson, 1978; Berg and Ström, 1998) and an official map based on aerial photos from 1959/1961 were used to assess the influence of management history on sward structure.

Data analysis

Several different standard statistical tests were used in the different studies, for details se Paper I-IV. In addition, ordination (software CANOCO 4.51, Biometris, 1997-2003) was used in the meadow bird census study (Paper I) and in the meadow vegetation study (Paper IV) in order to detect general responses of the species community (Jongman et al., 1995), and to detect highly intercorrelated variables. In the meadow bird study (Paper I), census sites within each wetland area were considered dependent (spatially autocorrelated) and, therefore, census sites belonging to the same wetland area were arranged together into blocks (n=5, used as covariates). The block structure focused the analysis on the environmental variables by reducing the influence of variation linked to meadow area location (ter Braak and Ŝmilauer, 2002). The importance of individual environmental variables was tested against the null-hypothesis of non-significant random variation by Monte Carlo permutation tests. Because of small sample sizes within wetland areas only residuals from the reduced model ('null model') were permuted, which reduce the risk for type I error (ter Braak and Ŝmilauer, 2002). For details see Paper I.

Generalized linear mixed models (GLMM) available in the GLIMMIX procedure (SAS Institute Inc., 2002-2003) were used in several studies (Paper I, II and IV). Model comparisons were performed according to Burnham and Andersson (2002), a information-theoretic approach assuming that several models (and variables) may explain species occurrence simultaneously. To assess strength of evidence and importance of environmental variables, we used Akaike's Information Criterion (AIC), which offers a possibility to rank models based on their balance between complexity and goodness of fit to the data (Burnham and Anderson, 2002). We followed the recommendation to make inference from several models, to increase the ability of interpretation if several models are competing. For details see Paper I, Paper II and Paper IV.

Results and Discussion

Meadow bird censuses (Paper I)

Redundancy analyses (Fig. 1) and single species models suggested habitat openness to be the most important factor for bird species composition on the studied inland wet meadows. Although some passerine species seemed to prefer shrub or partly forested habitats, species preferring open meadows decreased strongly in total abundance even at small amount of forest (0-5%) at the 250 m scale (Fig. 2). Such small amounts of forest were common at the meadow areas (varying between 30% and 86% of the sites among areas). A probable mechanism for the lower abundance of open habitat species (all ground nesting) is avoidance of edge habitats and mosaic landscape structures due to increased nest predation risk (Møller, 1989; Berg et al., 1992; Andrén, 1995). Thus, a major management option in many Swedish inland meadow areas is the clearing of woodlands in order to increase the area of open habitat.

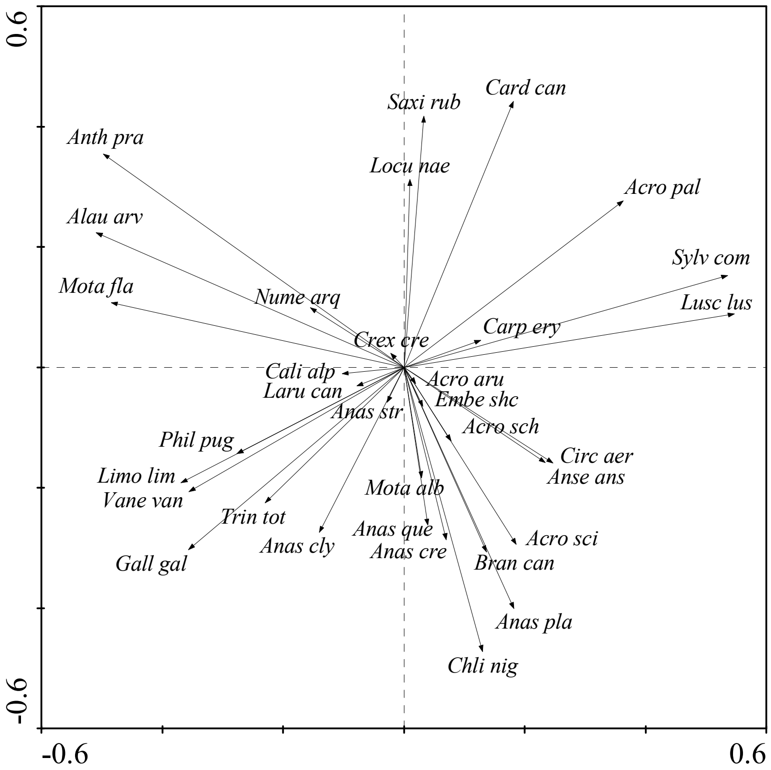

Fig. 1. Redundancy analysis (RDA) of the wet meadow bird community with standardized species correlations, where length of a species' arrow indicates measure of fit (R) with the ordination diagram.

The second major factor that affected bird community composition was wetness, with a gradient from dry to flooded meadows often adjacent to wetlands (Fig. 1). The effect of flooding was also evident among ducks and some wader species when comparing wet and dry years. Natural water fluctuations or wetness has previously been shown to be important for abundance of meadow birds (Milsom et al., 2000; Hart et al., 2002; Kleijn and Zuijlen, 2004; Smart et al., 2006). Wet areas provide habitats for many of these species with occurrence of aquatic prey, more accessible soil prey and more accessible surface prey due to reduced vegetation growth (Ausden et al., 2001). Thus, drainage may be a major threat to several meadow birds. For example, the general decrease in wetness of UK wet grasslands may have been a driving factor for declines in breeding waders during the last decades (Wilson et al., 2005). Large-scale water level regulations for conservation purposes are usually problematic since extensive areas of adjacent farmland owned by several landowners will be flooded. An interesting alternative is partial flooding of meadows from small tributary streams since small-scale topography and hydrology may have considerable positive effects on breeding wet meadow birds (see also Glaves, 1998; Ausden and Hirons, 2002). Large areas of Scandinavian meadows were historically managed to enhance flooding (damming, ditches) in order to increase hay production (Elveland, 1979; Emanuelsson and Johansson, 1987), and this management regime likely favoured the meadow birds at that time (Elveland and Sjöberg, 1982).

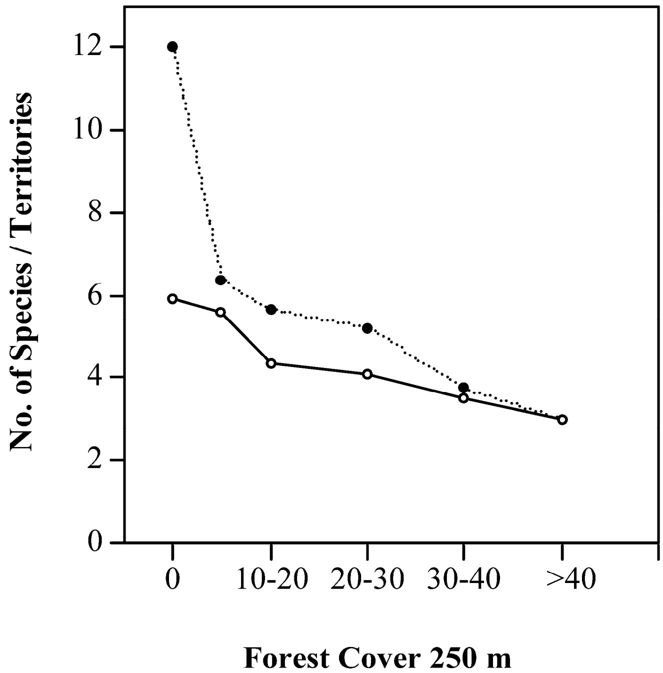

Fig. 2. Relationship between number of “open habitat species” (dotted line, linear regression, df=1, F=59.2, $p < 0.001$, R^2=0.30) and total abundance of open habitat species (solid line, df=1, F=49.4, $P < 0.001$, R^2=0.26) and amount of forest at the 250 m scale.

The redundancy analysis suggested that management regime and sward characteristics only had weak independent effects on the wet meadow bird community. The single species models indicated that six species were associated with management variables, while eleven species were associated with sward height variables. Earlier studies (Larsson, 1976; Milsom et al., 2000; Hellström and Berg, 2001;

Ottwall and Smith, 2006) also found that effects of management regimes on the bird fauna are weak or ambiguous. One probable reason for lack of strong associations with management is that the different management regimes are coarse classifications that do not include intensity and time of grazing and mowing.

In general, grazing had the highest cover of low sward (<5cm, positively associated with abundance of six species). Meadows managed by mowing and late season grazing had high cover of short to rather short swards, whereas mowing mainly resulted in rather tall to tall vegetation. Eleven species showed positive association to cover of rather short (5-15 cm) sward and seven species were positively associated to cover of rather tall swards (15-30 cm). However, also soil conditions and wetness influenced sward height and structure. Coarse-grained soils seemed to favour lower swards (<15 cm), while fine-grained soils were associated with high swards (>30 cm) and fast decline in of low sward between May and June. These results correspond to previous studies on soil fertility and wetland plant biomass (Smart and Barko, 1978; Keddy, 2000). Meadows with similar management but different fertility or wetness are therefore likely to develop different species composition and sward structure.

Mowing in combination with late season grazing alters marsh vegetation significantly more than management with mowing only (Bakker, 1978) and this management regime combines the positive effects of mowing (no destruction and disturbance of nests) and grazing (more heterogeneous sward structure), see Paper I. Mowing in combination with late season grazing resulted in sward of intermediate height, which was preferred by many bird species. In line with this, species richness of management-dependent species (species avoiding unmanaged areas and tall swards, see Paper I) was significantly associated to proportion managed with combined mowing and grazing. In contrast, species richness of these species was negatively associated with proportion managed by mowing and unmanaged areas. Thus, an increased use of mowing with late season grazing should affect species richness, abundance and reproductive success of management-dependent meadow species positively. Increased use of mowing might also be necessary in regions with shortage of cattle.

However, different bird species have different habitat preferences. Species associated with short sward (e.g. Lapwing and Dunlin *Calidris alpina schinzii*) are favoured by relatively intensive grazing, whereas mowing is more attractive for species associated with tall or rather tall sward (e.g. Sedge Warbler *Acrocephalus schoenobaenus*, Grasshopper Warbler *Locustella naevia* and Corncrake), see also Milsom et al. (2000). The avoidance of forested areas by several management dependent species, and increased predation rates close to edges, suggests that the most intensive management regimes (grazing and mowing combined with grazing) should preferably be targeted to landscapes with high qualities (see also Milsom et al., 2000), i.e. concentrated to large open meadow areas without woodland. In contrast, extensively managed areas could be situated in partly forested areas since meadow birds associated with unmanaged or tall sward did not seem to avoid areas adjacent to forests.

Corncrake study (Paper II)

Corncrakes in central Sweden preferred meadows to arable fields. Furthermore, vegetation height at meadows with corncrakes was also significantly higher (mean 60 cm) than at random meadow sites (mean 33 cm). Corncrakes preferred unmanaged meadows, avoided grazed meadows and used meadows managed by mowing as much as expected by their area. Management regime is strongly associated with vegetation height, and the tall vegetation in unmanaged sites and in some less intensively managed areas was strongly preferred by the corncrake.

In contrast to Corncrakes, most other meadow species in focus of management and conservation measures prefer vegetation of short or intermediate height, although nearby denser swards might be used for nesting (Beintema and Muskens, 1987; Chamberlain et al., 1999; Johansson, 2001; Bradbury and Bradter, 2004). In the future, there might be a shortage of suitable habitats for Corncrakes since abandoned areas become swamp forests dominated. Furthermore, our study suggests that vegetation is taller in areas that have been unmanaged for many years compared to areas that have been unmanaged for a few years (Fig. 3). Thus, present management regimes might result in polarized landscapes with intensively managed meadows and totally overgrown meadows in succession to forest.

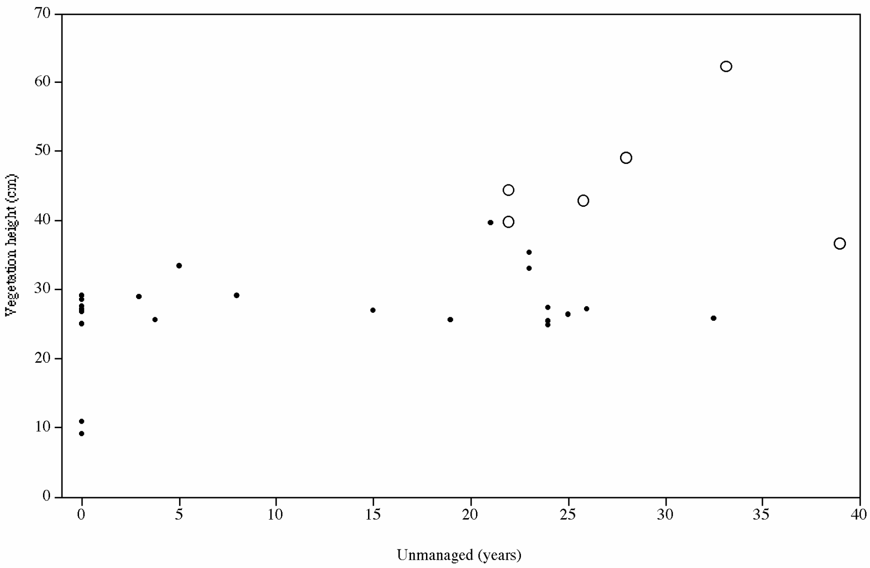

Fig. 3. Relationship between vegetation height and years without management during the last 40 years on the largest meadow (Nötmyran) at the Svartån site (Linear regression, df=1, F=12.9, P <0.001). Small filled dots represent meadow parcels without calling corncrakes and large unfilled dots (n=6) represent meadow parcels with calling corncrakes during 1999-2002.

In the present study most Corncrakes (58%) on meadows were found in areas without management schemes for the farmers. Furthermore, in managed meadows several corncrakes (62%) were found in restored areas managed for less than ten years of the last 40 years. Thus, subsidy schemes of wet meadows have probably not benefited Corncrakes, except in cases when overgrown areas have been cleared from shrubs and trees.

Sites where Corncrake territories occur regularly could be managed to maintain the tall vegetation suitable for the species. However, the results from our study suggest that yearly mowing for many years results in a vegetation structure that is avoided by Corncrakes. A possible management regime would therefore be mowing every few years, although the effect of different mowing frequencies on vegetation height and structure needs further studies in sites with different vegetation, nutrient supplies and water regimes. An important prerequisite for less intensive management regimes is that it is possible for the farmers to receive financial allowances for meadow management every year, even when meadows are managed every two years. At present, the allowance system focuses completely on yearly management (SJV, 2004), but meadow management regimes adapted for Corncrake conservation ought to be an important argument for the adoption of alternative management regimes.

Habitat selection and reproductive success of Yellow Wagtails (Paper III)

Breeding success of Yellow Wagtails was higher in mowed meadows, but densities of breeding pairs were similar in grazed and mowed meadows. However, breeding density benefited from mowing when environmental variables and management type were modelled together. Experimental nests suggested a similar pattern with higher probability of nest survival in mowed meadows, mainly because of absence of trampling by cattle, but possibly also due to lower nest predation risk.

The experimental results corresponded to a previous study by Flyckt (1999) on breeding performance of Yellow Wagtails in south Sweden. Because of cattle trampling on nests, the pairs breeding at grazed wet meadow sites produced 9% less of fledged young per clutch than pairs in mowed sites (Flyckt, 1999). Yellow Wagtail nest mortality due to cattle trampling has been found in other studies (Mason and Lyczynski, 1980; Dittberner and Dittberner, 1984; Bradbury and Bradter, 2004). Furthermore, increased density of livestock in grazed habitats has been suggested to be one important factor behind the continuous decline in Yellow Wagtail population numbers in pastoral parts of the UK (Chamberlain and Fuller, 2000; Vickery et al., 2001).

A correspondence in real and experimental nests success patterns suggested true differences between grazed and mowed meadows. We consider the experimental nest study to be useful because previously described sources of bias were reduced and the results were validated through comparison to natural breeding success (e.g. Ammon and Stacey, 1997; Willebrand and Marcström, 1998; Wilson et al., 1998; Pärt and Wretenberg, 2002). We suggest that experimental nest studies, in combination with estimates of natural breeding performance, are a useful approach for investigating patterns in habitat quality for species having cryptic nests.

Other variables associated with breeding success of real nests and breeding densities of Yellow Wagtails mainly correlated to humidity at meadow sites (i.e. distance to permanent water, flooding index). Yellow Wagtail territories have earlier been shown to be associated with the abundance of shallow pools and prolonged winter flooding, probably due to suitable feeding grounds (Bradbury and Bradter, 2004). Breeding density was also negatively associated with vegetation height variation, which was linked with less cover of low vegetation in our study site. Thus, because patches of sparse vegetation are important foraging grounds (Bradbury and Bradter, 2004) this could explain why heterogeneous vegetation structure might negatively influence breeding density. For breeding success, distance to forest was also a significant predictor, which may correspond to Yellow Wagtail selection of territories away from woodland edges, to avoid predators (Stiebel, 1997).

Grazing may create heterogeneity in vegetation that promotes important feeding grounds for wet meadow bird communities of high conservation value (e.g. Vickery et al., 2001), although destruction of nests due to trampling by cattle may decrease reproductive success (Beintema and Müskens, 1987). However, by temporal and spatial adjustment of grazing regimes, reproductive performance of wet meadow birds may increase due to decreased effects of trampling (Beintema and Müskens, 1987; Hart et al., 2002). Mowing of wet meadows (after main breeding period) is a promising alternative management method for Yellow Wagtail habitats. However, water level management is also important, i.e. to maintain shallow water and moist ground in wet meadows. For example, the general decrease in wetness of wet lowland grasslands in the UK may have been a driving factor for declines in breeding waders during the last decades (Wilson et al., 2005). Further, in Dutch wet meadows, high densities of breeding birds correlated significantly to higher groundwater tables (Kleijn and Zuijlen, 2004). However, maintaining a gradient from dry to moist conditions with pools of shallow water within Yellow Wagtail habitats may be necessary to buffer against stochastic events, e.g. by ensuring safe nest sites during rainy breeding seasons (Flyckt, 1999; Mason and Lyczynski, 1980).

Sward composition and environmental factors (Paper IV)

This study showed that moisture and soil fertility affected sward structure and sward composition in sites with similar management. A detrended correspondence analysis (DCA) showed that the first ordination axis was strongly associated with soil fertility, and that the second axis correlated with moist. Multi-model comparisons of species richness and abundance of plant "taxa" suggested that moisture or flooding were associated with low species richness of vascular plants, low abundance of herbs and high abundance of sedges & rushes. Furthermore, high soil nutrient levels were associated with abundance of grasses (possibly also forbs), and negatively associated with abundance of sedges & rushes. Thus, similar management regimes might result in swards of different composition and structure in different sites due to different site conditions.

Sward components were influenced by small-scale environmental conditions, which indirectly might influence the meadow bird communities Species-richness and abundance of bird species associated with "low-intensity management" (i.e. management with resting periods) were positively correlated to nutrient levels, soil reaction, sward height and litter depth, suggesting that suitable conditions for these species is found in less intensively managed areas, where fertile soils and relatively thick litter results in a high vegetation (Wheeler and Shaw, 1991). In contrast, bird species associated with "continuous management" showed correlations to fewer sward variables, although abundance was positively associated with abundance of forbs and occurrence of surface water. Differences in nutrients between the sources for meadow wetness (surface water and ground water) might create a variation in swards (Palczynski, 1984). We interpret the association with forbs as a preference for heterogeneous swards (see also Vickery et al., 2001; McCracken and Tallowin 2004; Atkinson et al., 2005), which are attractive nest sites and good foraging areas. The abundance of forbs was negatively associated with management time, suggesting that long-term continuous management in our study area might create swards that are less attractive for management dependent species. In general the correlation in abundance between the seven management dependent bird species were fewer and not as strong (n=3, mean r_s=0.54 and p <0.05) as between the "low-intensity management" species (n=9, mean r_s=0.65 and p <0.01), suggesting that the species-specific habitat requirements were more important for the management dependent species.

Effects of management history on sward characteristics included a positive association between number of management years and cover of mosses, and abundance of sedges & rushes, and a negative association with abundance of forbs. No direct associations were found between abundance and species richness of the two groups of birds, despite correlations to abundance of different vascular plant "taxa" (which in turn showed associations to management history). However, as other factors (present management regime, nutrient conditions, flooding, occurrence of surface water) also affects swards structure, the limited sample size made it difficult to establish these relationships.

A fundamental effect of management on herbaceous and grassy field layer vegetation is the decrease of litter. Litter depth was positively associated with vegetation height, and negatively associated with species richness and abundance of grasses. However, effects of litter accumulation on sward composition have been contradictory, probably due to time lags, which for example result in short term (a few years) decrease and long term increase of above ground biomass, respectively (Xiong and Nilsson, 1999). A study of reproductive success and seedling establishment of vascular plants in the same meadow area (Norkvist, 2002) showed that fewer seedlings established in grazed areas than in areas managed by mowing or by mowing combined with late season grazing. This was interpreted as an effect of lower production of seeds in grazed areas than in areas with other management regimes. However, mowing produced more litter and taller vegetation in the late season, and litter depth above one cm had an adverse effect on seedling establishment. Thus, the best conditions for seedling establishment are found in areas with high production of seeds, at least a thin litter cover and low vegetation. These conditions develop in areas managed by mowing combined with late season grazing (Lennartsson and Oostermeijer, 2001; Norkvist, 2002), which also is the traditional management regime in Scandinavia.

Conclusions

Habitat openness was the most important factor for bird species composition on the studied inland wet meadows. Although some passerine species preferred shrub or partly forested habitats, species preferring open meadows decreased strongly in abundance in landscapes with small amounts of forest. Thus, a major management option in many Swedish inland meadow areas is the clearing of woodlands in order to increase the area of open habitat. The second major factor that affected bird community composition was wetness. Large-scale water level regulations for conservation purposes are usually problematic since extensive areas of adjacent farmland owned by several landowners will be flooded. An interesting alternative is partial flooding of meadows from small tributary streams (used historically), since small-scale topography and hydrology may have considerable positive effects on breeding wet meadow birds.

Management regimes and sward characteristics were suggested to have weaker effects on the wet meadow bird community. Most species showed positive association to cover of swards of intermediate heights (5-30 cm), which correlated to mowing and late season grazing, although mowing also correlated to tall vegetation. In contrast, grazing had the highest cover of low sward (<5cm), which was positively associated with few species. Thus, increased use of mowing (or mowing combined with late season grazing) should be positive for species associated with swards of intermediate heights. Furthermore, mowed meadows were suggested to be of higher quality than grazed meadows, since reproductive success of Yellow Wagtails was higher in mowed than grazed sites, due to lack of nest losses due to trampling and possibly lower nest predation rates.

Corncrakes preferred mowed areas to grazed areas, although unmanaged areas had the highest corncrake densities. Furthermore, continuous management with mowing resulted in short vegetation, which was avoided by the corncrake, suggesting that effects on the bird fauna of alternative management regimes, such as mowing every few years, should be further evaluated. However, different bird species have different habitat preferences and species associated with short swards were favoured by intensive grazing. The avoidance of forested areas by several management dependent species, and increased predation rates close to edges, suggests that the most intensive management regimes (grazing and mowing combined with grazing) should preferably be concentrated to large open meadow areas without woodland. In contrast, "low-intensity management" of meadows could be performed in partly forested areas since meadow birds associated with unmanaged or tall sward did not seem to avoid areas adjacent to forests.

Also soil conditions and wetness influenced sward height and structure. High soil nutrient levels were associated with abundance of grasses (also forbs), and negatively associated with abundance of sedges and rushes. Species-richness and abundance of bird species associated with "low-intensity management" correlated positively to nutrient levels, soil reaction, sward height and litter depth, suggesting that suitable conditions for these species is created in less intensively managed areas (e.g. managed by mowing), where fertile soils and relatively thick litter results in a high vegetation. Bird species associated with "continuous management" showed correlations to few sward variables, although abundance was positively associated with abundance of forbs. The abundance of forbs was negatively associated with length of management period (opposite pattern for sedges and rushes), suggesting that long-term continuous management might create swards that are less attractive for management dependent birds. In conclusion meadows with different fertility or wetness are likely to develop different species composition and sward structure, despite similar management. Heterogeneous meadow swards structure which benefits several meadow birds could possibly be maintained by different mowing regimes.

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